Dispersal of *Homalodisca vitripennis* (Homoptera: Cicacellidae) from a Point Release Site in Citrus

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ABSTRACT The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), is an important vector of *Xylella fastidiosa* Wells et al., a bacterium that has caused substantial losses in the viticulture and ornamental industries in California. Area-wide management programs have been implemented to reduce vector populations and limit the spread of this disease. However, there is still a lack of information on the factors that influence this insect's movement within and between host crops. In this study, we used mark-release-recapture (MRR) to examine the dispersal of *H. vitripennis* in a mature orange grove, *Citrus sinensis* Osbeck. Insects were doubly marked with chicken or rabbit immunoglobulin G (IgG) proteins and fluorescent dusts to enable monitoring over several weeks. Our objectives were to examine the reliability of IgG protein markers relative to fluorescent dusts, determine how sharpshooter movement differed in this landscape relative to a previous study, and develop a better understanding of the biotic and abiotic factors that could influence sharpshooter dispersal. Linear regressions of recapture data with a diffusion model provided significant fits to the data in five of six releases. Recapture data were fitted to a diffusion model, and based on parameters generated with the model, estimated dispersal distances for *H. vitripennis* at 72 h showed 50 and 99% remained within annuli of 31 and 150 m from the release site, respectively. Flight activity was greatest between 1000 and 1400 hours, and no flights occurred between 2200 and 0600 hours. Only temperature explained a significant amount of the variability in recapture of *H. vitripennis*, with sharpshooters rarely trapped below 18°C.

KEY WORDS *Homalodisca coagulata*, IgG protein markers, fluorescent dust, mark-release-recapture, diffusion model

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Takiya et al. 2006), previously known as *H. coagulata* (Say), has spread rapidly throughout southern California since its introduction in 1989 (Blua et al. 1999, 2001, Sorenson and Gill 1996, CDFA 2005). This insect feeds on a wide variety of ornamental and crop plants and in the process transmits the bacterium, *Xylella fastidiosa* Wells et al., which is the causal agent of Pierce's disease (PD), as well as several other diseases (Purcell 1979, Purcell et al. 1979, 1999, Redak et al. 2004). Losses caused by PD have been estimated to be in excess of $13 million for Riverside County alone (Wine Institute 2001), and at least 13 other counties are now known to be infested with *H. vitripennis*.

Areawide management programs have been instituted in an effort to limit the spread of PD and *H. vitripennis* (National Research Council 2004). Although these programs have been relatively successful, *H. vitripennis* can still be found in large numbers in citrus and other horticultural and ornamental crops in southern California (Blua and Morgan 2003). Citrus offers stable feeding and oviposition sites throughout the year, and at some locations, the incidence of PD in vineyards has been found to be related to its proximity to citrus (Perring et al. 2001). In recent years, because of economic factors, many citrus orchards have been removed in southern California, while new plantings have increased in the southern San Joaquin Valley (CASS 2004). With this expansion of citrus into the more sensitive grape-growing regions of the state, we need to have a better understanding of the factors that limit or enhance the dispersal of *H. vitripennis* in citrus. An enhanced knowledge of the role of biotic and abiotic factors might enable us to design better management programs in which high risk areas could be delineated where climatic factors favor the expansion of sharpshooters. Alternatively, strategic placement of certain hosts might be used to mitigate sharpshooter movement.

Previously, we compared the dispersal of *H. vitripennis* with that of a native California sharpshooter,

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Homalodisca liturata Ball (Burks and Redak 2003). The setting for this study was over bare ground with widely spaced abandoned alfalfa (Blackmer et al. 2004). Under these conditions, both species readily dispersed to traps located at the furthest annulus (90 m) and up to the highest trap elevation (7 m). Linear regressions of recapture data with a diffusion model provided significant fits to the data with high coefficients of determination for all *H. vitripennis* releases and for three of four *H. liturata* releases, suggesting that their movement could be described by a diffusion process. In terms of the environmental parameters measured, only wind speeds in excess of 3 m/s reduced takeoff activity and subsequent trap catch.

In this study, we conducted a similar experiment with *H. vitripennis* in a mature orange grove. In this setting, more opportunities for alighting, feeding, and oviposition, as well as substantial differences in environmental conditions (i.e., wind speed, temperature, and humidity), could influence the rate and extent of movement. Recapture data generated in this study were fitted to the diffusion model (Turchin and Thoeny 1993, Turchin 1998) used in our previous study (Blackmer et al. 2004). Based on parameters generated from the diffusion model, estimates of dispersal distance were calculated. We also measured sharpshooter movement relative to time of day and environmental conditions and compared the efficiency of two marking techniques (IgG proteins and fluorescent dusts).

Materials and Methods

Release Site and Insect Collections. The release-recapture site was located at 34°24′ N, 118°44′ W in an 11-ha mature (≈6 m in height) Valencia orange grove, *Citrus sinensis* Osbeck, near Fillmore, CA. The field was bordered on the west by a 20-ha fallow field, to the east it was separated from a 25-ha orange grove by a row of eucalyptus trees (≈30 m in height), and to the south and north it was bordered by 8- and 15-ha orange groves, respectively. There was a large resident population of adult *H. vitripennis* at this site, which were trapped concurrently with our marked sharpshooters. Temperature, relative humidity, barometric pressure, rainfall, dew point, wind speed, and wind direction were monitored at the release site at 30-min intervals from July through October 2002 with a portable weather station (Vantage Pro. 6150C; Davis Instruments, Hayward, CA).

The morning of each release, adult glassy-winged sharpshooters were collected from young *C. sinensis* trees that were located 5 km from the release site. Terminal branches containing sharpshooters were shaken into 38-cm-diameter by 84-cm sweep nets (7212CM; BioQuip Products, Gardena, CA). The contents of the sweep nets were dumped into preweighed paper sacks, which were folded at the top, stapled, and placed in ice chests. After several thousand sharpshooters had been collected in the paper sacks, their weight was determined by subtracting the weight of the paper sack and leaf litter. Sharpshooters were emptied into fine-mesh bags (Blackmer et al. 2004) that facilitated the application of IgG protein solutions. To obtain an estimate of the number of sharpshooters released, subsamples of sharpshooters ($N \geq 100$) were randomly collected from our samples before the IgG protein solution and fluorescent dusts were applied. These sharpshooters were placed in 30-ml vials, stored on dry ice, and weighed individually in the laboratory. The number of sharpshooters released was determined by dividing the weight of sharpshooters in the paper sacks by the mean individual sharpshooter weight. Prerelease sex ratios also were determined from these subsamples, and at the end of the release, sharpshooters that had not left the release area were collected to determine the sex ratio of the population that remained.

IgG Protein and Fluorescent Marking. A double action internal mix airbrush set (Paasche Airbrush Co., Harwood Heights, IL) connected to a portable air tank was used to apply a fine mist of 1.0 mg/ml solution of rabbit IgG (no. I5006; Sigma-Aldrich, St. Louis, MO) or chicken IgG (no. I4881; Sigma-Aldrich) to the sharpshooters (Hagler et al. 1992, Hagler 1997a). We previously determined that these markers were detectable on *H. vitripennis* for up to 19 d under field conditions (Blackmer et al. 2004). After the water evaporated, glassy-winged sharpshooters were placed in 5-liter plastic containers with 0.5 g of fluorescent dust. The containers were rotated gently until the sharpshooters had a light coating of dust. A subsample of 100 sharpshooters was placed on dry ice, and effectiveness of fluorescent marking was examined in the laboratory. For all releases, fluorescent marking was detectable under UV light on 100% of the individuals examined. Each release had a unique combination of chicken or rabbit IgG protein and a fluorescent dust so that we could monitor sharpshooter movement for several weeks. The following combinations were used sequentially: release 1 (week 1), rabbit IgG and fire orange; release 2 (week 3), rabbit IgG and horizon blue; release 3 (week 5), chicken IgG and signal green; release 4 (week 7), chicken IgG and corona magenta; release 5 (week 9), rabbit IgG and horizon blue; release 6 (week 11), rabbit IgG and signal green; release 7 (week 13), rabbit IgG and fire orange. With this sequence of markers, at least 6 wk passed before the same fluorescent dust was used again. Fluorescent-marked sharpshooters of a particular color were recovered on our traps up to 4 wk after release.

Releases and Recapture Layout. Releases were made every 2 wk from 10 July through 1 October 2002. Sharpshooters were released from a shaded, 15-cm-high platform placed in the center of the citrus grove. All releases began between 1300 and 1600 hours, and the initial recapture interval was 72 h long. This time interval was decided on because very few fluorescent-marked individuals were observed on the most distant traps until ≈72 h after release. Marked sharpshooters, for a given protein/fluorescent dust combination, continued to be captured 2 and 4 wk after their initial release. Trapping periods for these later recaptures

were also 72 h long and were represented by the trapping intervals 336–408 and 672–744 h after their initial release.

Collection poles and traps were as described in Blackmer et al. (2004), and consisted of three 3-m lengths of polyvinyl chloride (PVC) tubing of varying diameters (3.5, 5, and 6.5 cm diameter) that could be raised to 7 m or retracted for transport. A pulley system enabled us to raise and lower sticky traps without taking poles down between releases. Forty-eight poles were placed in the field in a grid pattern surrounding the central release point. To enhance recapture rates, more poles were placed at the furthest distances, with six poles at 12–22 m, 18 at 25–45 m, and 24 at 46–78 m from the central release point. Additional traps ($N = 9$) were set up just north of the recapture grid to monitor sharpshooter movement within the orchard relative to time of day and environmental parameters. These traps were positioned 1 m above the ground and 16 m apart and were changed at 4-h intervals from 0600 to 2200 hours during one 24-h period for each release. For each 4-h period, sharpshooters were counted, and sex was determined.

Yellow sticky traps were cut to 40 by 60 cm from Pestick high-density plastic sheeting (Bright Yellow, Cat. No.01–4000-1; Hummert International, Earth City, MO) and hand rolled with a heavy coating of Pestick. Approximately 16–18 h before each release, sticky traps were labeled according to height and distance from the central release site and raised on the poles. Each trap was positioned around the PVC poles to form a 16-cm-diameter cylindrical trap that could be raised and lowered by the pulley system. Traps were held in place by 26-mm-wide binder clips that connected to the top and bottom edge of each trap. Each pole contained three traps positioned at 1, 3.5, and 6 m above ground. The 3.5-m traps were at midcanopy and the 6-m traps were just above canopy. At the end of each 72-h recapture period, sticky traps were collected, covered with wax paper, and transported back to the laboratory where the sharpshooters were counted and processed. A Blak-Ray longwave-UV lamp (ML-49; UVP, Upland, CA) equipped with a blacklight bulb (F6T5/BLB) was used to sort individuals that had been marked with fluorescent dusts. Marked individuals were counted, sexed, placed in centrifuge tubes, and stored at −70°C in an ultracold freezer until they could be analyzed by enzyme-linked immunosorbent assay (ELISA) for IgG proteins. For each release, an additional randomly selected subsample (minimum of 100 per trap) of sharpshooters was tested for the presence of rabbit or chicken IgG proteins. This would determine whether some individuals had been marked sufficiently with the IgG protein but had not been marked adequately with fluorescent dusts and vice versa. Because of time constraints and the fact that most sharpshooters were recaptured on traps close to the release site, only the 24 closest traps were processed for both IgG and fluorescent dusts for each release. All traps were processed for fluorescent dust.

ELISA. Positive, time 0 controls for ELISAs were removed from the collections after the rabbit or chicken IgG and fluorescent dust had been applied. Unmarked sharpshooters served as our negative controls. These sharpshooters were placed in 30-ml vials, transported to the laboratory on dry ice, and stored in a −70°C ultracold freezer until they could be processed. Sharpshooters that were recaptured on the sticky traps were removed, placed in microcentrifuge tubes with 500 μl of phosphate-buffered saline (PBS, pH 7.3), agitated overnight on a shaker, and assayed for the presence of rabbit and chicken IgG proteins by the protein sandwich ELISAs as described previously (Hagler 1997b, Blackmer et al. 2004). Mean (±SD) absorbance values were calculated for the negative controls. Individual field-collected sharpshooters were scored positive for rabbit IgG or chicken IgG protein if the absorbance value was 3 SD above the negative control mean (Hagler 1997b).

Analyses and Fitting Diffusion Model. Unless otherwise noted, all analyses were conducted with SAS (Version 8; SAS Institute 1999). The relationship between sharpshooters trapped and environmental parameters (wind speed and wind direction, temperature, dew point, rainfall, relative humidity, and barometric pressure) were analyzed by multiple linear regression analyses (stepwise regression). The relationship between sharpshooters trapped relative to collection date and time of day was analyzed by two-way analysis of variance (ANOVA). Recapture rates of *H. vitripennis* relative to cardinal direction, distance, height, release date, and their interaction were examined using multiple linear regression models (stepwise regression; model 1). The distribution of resident sharpshooters was also analyzed by regression analysis relative to cardinal position in the field, trap height, and collection date. PROC univariate residual analysis was used to check whether data met the assumptions of normality and homogeneity of variance. Recapture counts were transformed by $\sqrt{Y + 0.5}$ and resident counts by $\log(Y + 1)$ before analyses.

Recapture data generated from these studies were also fitted to a diffusion model, and model results were used to estimate dispersal distances for *H. vitripennis* in the mature orange grove. The assumption of no directionality in dispersal was tested before fitting the recapture data to the diffusion model. The average displacement direction of recaptured sharpshooters was calculated for each of the releases with equation 1 taken from Turchin and Thoeny 1993:

$$X_j = \frac{\sum_{i=1}^{n} x_i C_{ij}}{\sum_{i=1}^{n} C_{ij}} \qquad [1]$$

where C_{ij} is the cumulative recaptures in trap i over the course of recapture day j, x_i is the x coordinate of trap location i relative to the central release point, and n is the number of traps. The quantity $x_i C_{ij}$ is the sum

of the recapture displacements along the *x*-axis for all sharpshooters that flew to trap *i*. This equation provides the average displacement X_j, along the *x* coordinate. The average displacements along the *y* coordinate were calculated in the same manner. Taken together, the average displacements along the *x* and *y* coordinate give the mean displacement of recaptures within the grid. The average displacement of recaptures for each replicate release was tested by *t*-test to determine if they were significantly different from zero along the *x*- and *y*-axes (Sokal and Rohlf 1981). Differential dispersal by male and female sharpshooters was also evaluated before fitting the model. The sex ratio of recaptured individuals was arcsine transformed, and linear regression analysis was used to determine if a significant relationship existed between the sex ratio and dispersal distance.

After calculating the net displacement direction and the potential differential dispersal relative to sex, the recapture data were fitted to a statistical model based on the assumption that sharpshooter movement could be explained by a diffusion process. The diffusion model developed by Turchin and Thoeny (1993) was used and is defined as follows:

$$N = \mathrm{A}r^{-1/2}\exp(-r/\mathrm{B}) \qquad [2]$$

where N is the total number of recaptured sharpshooters dispersing to distance r, and $\mathrm{A} = \alpha N_0(8\pi)^{-1/2}(\mathrm{D}^3\delta)^{-1/4}$, a scale parameter that is proportional to the total number of sharpshooters released multiplied by the recapture efficiency of the trap. Parameter $\mathrm{B} = (\mathrm{D}/\delta)^{1/2}$, which measures the spatial scale of dispersal and is proportional to the square root of the diffusion rate (D = diffusion coefficient) divided by the loss rate (δ). To estimate the diffusion coefficient, it is necessary to know either the recapture efficiency (α) or the loss rate (δ). Neither of these parameters is known here, but it is still possible to estimate the fit of the recapture data to the model. To fit the diffusion model, equation 2 was linearized by taking the natural logarithm of both sides of the equation, which resulted in the following equation:

$$\mathrm{Log}(N) + \mathrm{Log}(r^{1/2}) = \mathrm{Log}(\mathrm{A}) - r/(\mathrm{B}) \qquad [3]$$

The recapture data were fitted with linear regression to equation 3 to estimate parameters A and B. To eliminate the problem of log-transforming zero values, recaptures at equivalent distances were averaged, and these averaged trap recaptures were log-transformed. The normal procedure of adding a small number before log transformation is inappropriate as it changes the form of equation 3, which results in the loss of biological meaning of parameters A and B (Turchin and Thoeny 1993).

We calculated the median dispersal distance $r_{0.5}$, the radius of a circle that enclosed 50% of the dispersers, using equation 4 derived by Turchin and Thoeny (1993) and the mean value of parameter B estimated from the regression of equation 3, using Mathematica (Wolfram 1988). Similarly, we calculated $r_{0.67}$, $r_{0.95}$, and $r_{0.99}$, the radii enclosing 67, 95, and 99% of the dispersers, respectively.

$$\frac{\int_0^{r_i} r^{1/2}\exp[-r/\mathrm{B}]\,dr}{\int_0^{\infty} r^{1/2}\exp[-r/\mathrm{B}]\,dr} = 0.5 \qquad [4]$$

Results

Release Statistics and Population Structure. Approximately 12,000 *H. vitripennis* were marked and released for each of the seven releases. High mortality occurred in the first release, and cooler temperatures occurred with the last release, resulting in low recapture rates for these two trials. A determination of sex ratios before the releases showed a slight male bias (1.2:1.0). Recapture sex ratios always showed a female bias (1.0:1.4), because fewer males were leaving the release site. Sex ratios of dead sharpshooters in the release site debris were always male biased (1.4:1.0).

During the MRR studies, only 1.2 mm of rain occurred. Temperatures averaged 20.5 ± 1.9°C, relative humidity was 70.3 ± 7.0%, and dewpoint was 12.9 ± 1.4°C. Winds were usually from the WSW and varied over the course of the day with a mean of 0.7 ± 0.1 m/s and a mean maximum wind speed of 2.7 ± 0.3 m/s.

Recaptures. More than 83,000 glassy-winged sharpshooters were marked and released between July and early October. Of these, when combined over all releases, 1,421 sharpshooters (or 70.1%) were recaptured within the first 72-h interval; 461 (or 22.7%) additional individuals were recaptured 408 h later, and 146 (or 7.2%) additional individuals were recaptured 744 h after their initial release. The average recapture rate, for marked individuals, after 744 h (or 4 wk) was 2.4%. High recapture rates were evident near the release site at 72 h, gradually expanded outward by 408 h, with reduced recaptures because of disappearance (either by death or emigration) being apparent by 744 h (Fig. 1).

On average, 1.0 ± 0.1 marked male and 1.4 ± 0.1 marked females were recaptured per trap, with 71 and 63% of these recaptured within 20 m of the release site, respectively (Table 1). The resident population of sharpshooters averaged 182.7 ± 8.2 per trap and increased in numbers from the center to the outside edge of the orchard, suggestive of an edge effect. The number of resident sharpshooters was greatest during July and early August and declined to an average of 28 per trap in early October. The majority of sharpshooters, whether marked or unmarked, were trapped on the 1- and 3.5-m-high traps (Table 1). Approximately 94% of the marked males, 90% of the marked females, and 81% of the resident population were trapped at 3.5 m or below.

Fluorescent Marked and ELISA Assay Comparisons. Of the >2,000 dusted sharpshooters examined, ≈73% were also positive for one of the IgG markers;

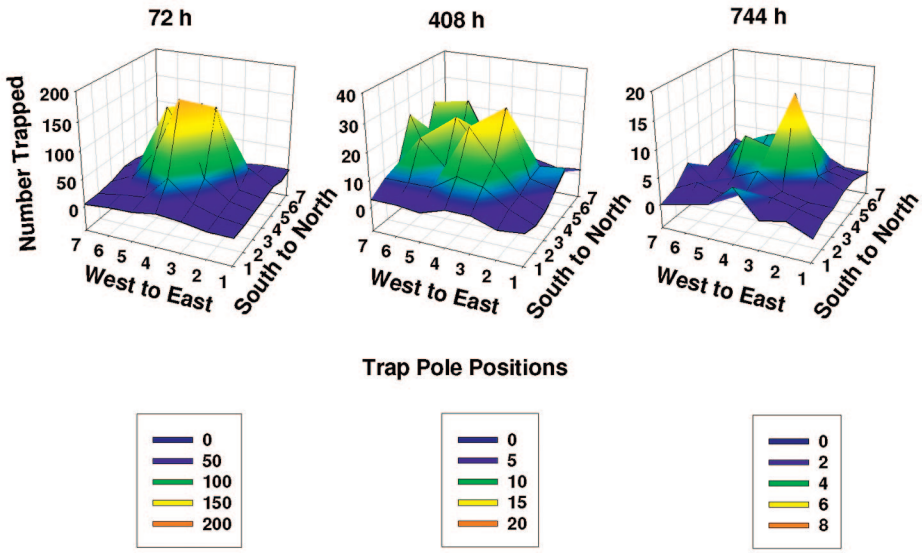

Fig. 1. Three-dimensional plots of the number of *H. vitripennis* recaptured on yellow sticky traps positioned on poles placed ≈18 m apart and collected at 72, 408, and 744 h after release from a central release site in an orange grove, Fillmore, CA, 2002. Numbers 1–7 represent pole positions from east to west or south to north in the orchard.

27% of the individuals were only positive for fluorescent dust. Individuals marked with chicken IgG and dust were positive for both markers 83% of the time, and individuals marked with rabbit IgG and dust were positive for both markers 65% of the time. At the 72-h time interval, both IgG and dust were detected 88.3% of the the time, at 408 h both IgG and dust were detected 34.6% of the time, and by 744 h, IgG and dust were detected in only 15.6% of the individuals. An additional 14,778 sharpshooters that did not contain fluorescent dust were selected from nearby traps (12–26 m from release site) and assayed for IgG markers. Approximately 4.2% of these individuals tested positive for chicken or rabbit IgG even though they were negative for dust.

Table 1. Mean number of marked and unmarked (=resident) *H. vitripennis* trapped on yellow sticky traps at varying distances and heights during six MRR trials conducted at Fillmore, CA, 2002

Variable	Fluorescent ± SE		Unmarked ± SE
	Male	Female	Total
Distance (m)			
10–20	4.13 ± 0.54	4.77 ± 0.55	164.70 ± 17.10
21–40	1.06 ± 0.11	1.61 ± 0.15	170.28 ± 9.96
41–60	0.37 ± 0.04	0.66 ± 0.07	189.36 ± 9.51
61–80	0.24 ± 0.06	0.56 ± 0.14	206.36 ± 16.94
Height (m)			
1	1.86 ± 0.19	2.00 ± 0.20	237.99 ± 9.81
3.5	0.83 ± 0.10	1.71 ± 0.18	209.98 ± 12.27
6.0	0.18 ± 0.03	0.40 ± 0.05	103.18 ± 6.96
Release date			
10 July	0.01 ± 0.01	0.04 ± 0.02	262.28 ± 12.74
23 July	0.90 ± 0.17	1.22 ± 0.16	473.85 ± 14.29
6 Aug.	0.59 ± 0.14	0.80 ± 0.13	256.68 ± 9.53
20 Aug.	1.06 ± 0.23	1.44 ± 0.23	101.40 ± 6.34
4 Sept.	1.27 ± 0.20	1.62 ± 0.21	133.74 ± 5.20
17 Sept.	1.73 ± 0.27	2.93 ± 0.37	109.03 ± 7.57
1 Oct.	0.18 ± 0.05	0.20 ± 0.05	27.59 ± 2.48

Regression Analyses and Fitting Diffusion Model to Sharpshooter Dispersal. Regression analyses for the resident population of glassy-winged sharpshooters indicated that collection date accounted for 53% of the variability in trap catch ($F = 956.0$; df = 1,862; $P < 0.0001$), trap height explained 9% of the variability ($F = 707.5$; df = 1,862; $P < 0.0001$), and distance explained <1% of the variability ($F = 493.4$; df = 1,862; $P < 0.0001$). The distance × height interaction was not significant, nor was the position of the trap in the field. For marked sharpshooters recaptured at 72 h, trap height was the best predictor of number of *H. vitripennis* recaptured ($r^2 = 0.37$; $F = 211.5$; df = 1,718; $P < 0.0001$). The addition of a distance × height interaction term explained an additional 6% of the variability ($F = 180.9$; df = 1,718; $P < 0.0001$) and cardinal direction accounted for only 1.6% of the variation in trap catch ($F = 191.8$; df = 1,718; $P < 0.0001$). The significant distance × height interaction was a result of recaptures being higher on lower traps close to the central release site. Release date and trap distance did not explain a significant amount of the variability in total trap catch ($P > 0.05$). When sharpshooters recaptured at 72, 408, and 744 h were combined, results varied little from the 72-h recaptures. A linear combination of height, distance × height interaction, and cardinal direction accounted for 46.7% of the variability in trap catch; a 2.1% increase over the 72-h recaptures.

The analysis of mean recapture displacements (equation 1, for *H. vitripennis* showed that there was no statistically significant shift along the x- or y-axis (Xj = −0.32 ± 1.28 m, $t = 0.25$; df = 5; $P = 0.81$; Yj = −3.23 ± 1.71 m, $t = 1.89$; df = 5; $P = 0.12$). Approximately 42% of the recaptured *H. vitripennis* were male. Linear regression of sex ratios relative to dis-

Table 2. Number of fluorescent-marked *H. vitripennis* released and recaptured, as well as parameter estimates of a diffusion model (equation 2) fit to 72-h recapture data from six MRR trials conducted in Fillmore, CA, 2002

Release[a]	Number released	Number recaptured	Percentage recaptured[b]	Parameter estimates			
				A	B	*P*	R^2
2	15,707	298	1.9	33.27	39.68	0.012	0.68
3	14,585	182	1.2	40.79	22.03	0.0012	0.90
4	18,790	267	1.4	41.75	27.60	0.011	0.76
5	14,563	341	2.3	104.10	17.87	0.001	0.99
6	12,930	308	2.4	58.31	22.95	0.009	0.71
7	6,676	25	0.4	2.84	39.00	0.204	0.30

[a] Release 1 was not used for mean parameter calculations because of low release rates.
[b] Percentage recaptured at 72 h for the fluorescent pigment used in a given release.

tance revealed no significant effect ($F = 1.67$; df = 1,43; $P = 0.20$). Therefore, to fit the recapture data, sexes were combined.

Linear regressions of the 72-h- recapture data with the diffusion model provided significant fits to the data with high coefficients of determination (R^2) for five of six releases (Table 2; Fig. 2). Calculations of dispersal distances for these releases showed that 50, 67, 95, and 99% of *H. vitripennis* remained within annuli of 31, 45, 103, and 150 m in 72 h, respectively.

Flight Activity Relative to Time of Day and Environmental Parameters. Significantly more sharpshooters were trapped between 1000 and 1400 hours relative to other 4-h sampling intervals (Fig. 3; $F = 129.8$; df = 4,224; $P < 0.0001$). No activity was detected between 2000 and 0600 hours. Of the environmental parameters examined, only temperature explained a significant amount of the variability in trap catch in the citrus setting (Fig. 4; $r^2 = 0.62$; $P < 0.0001$). Sharpshooters were rarely trapped when temperatures fell below 18°C. None of the other environmental parameters explained a significant amount of the variability in trap catch.

Discussion

Landscape composition can influence the distribution and movement of insects. While movement across an open landscape can be fairly rapid and linear, structurally complex landscapes can lead to slow and circuitous movement (Zalucki and Kitching 1982, Crist et al. 1992, Jonsen and Taylor 2000, Haynes and Cronin 2003, 2006). The latter response can be fairly involved and may be influenced by variations in environmental parameters, the insects physiological state, plant composition, and whether the plant serves as a resource for the insect. Previously, we examined factors influencing the movement of *H. vitripennis* and *H. lacerta* across an open landscape that consisted of large areas of bare ground with scattered, abandoned alfalfa plants. In this setting, movement was rapid and direct (J.L.B., unpublished data), and resulted in a relatively high recapture rate (12%) within a 6-h period (Blackmer et al. 2004). Recapture data were fitted to a diffusion model (equation 2 from Turchin and Thoeny 1993), and both species movement in this landscape could be explained by a diffusion process. Furthermore, by monitoring takeoff rates of these two species

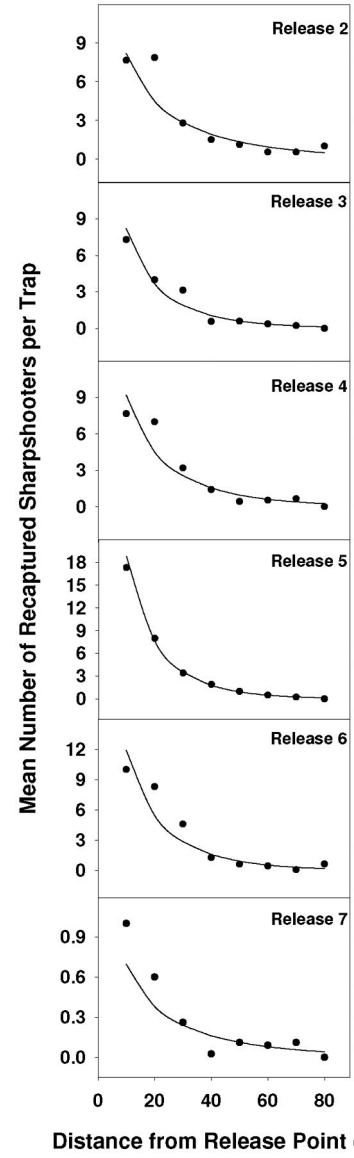

Fig. 2. Mean number of *H. vitripennis* recaptured after 72 h at varying distances from a central release point for each release. Data points are the average recaptures per trap at each distance. The solid lines are fitted curves to equation 2, using parameter estimates for *A* and *B* from each release.

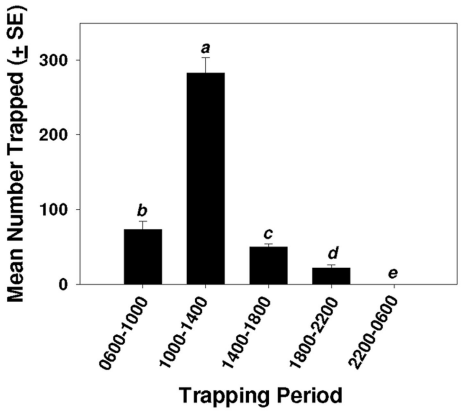

Fig. 3. Mean number of *H. vitripennis* trapped on yellow sticky traps at varying times of the day from 0600 to 2200 hours. Letters above error bars indicate significant differences.

relative to environmental parameters, we determined that only wind speed explained a significant amount of the variability in their flight initiation. Wind speeds >3 m/s inhibited takeoff activity in this setting.

The above situation would be encountered as *H. vitripennis* moves between host plants. Generally, these polyphagous insects engage in seasonal movements among a wide range of host plants (Mizell and French 1987, Brodbeck et al. 1990). However, a greater part of their time is spent in crops (i.e., citrus) where mating, oviposition, and feeding occur. This landscape would differ markedly from the previous landscape in terms of its structural complexity. Such differences could lead to variations in lighting, temperature, and protection from the wind and rain. Although our two studies were conducted in consecutive years and were located two hours distant from one another, temperature (i.e., 21–24°C), and rainfall patterns (i.e., trace) were similar between years, at least during July and August when direct comparisons could be made. However, measurements of mean and maximum wind speeds at the release sites were markedly different. In the open landscape, mean and maximum wind speeds were 3.9 ± 4.1 and 6.9 ± 6.0 m/s, whereas in the citrus grove, they were 0.8 ± 1.0 and 3.0 ± 2.7 m/s, respectively. Variations in these environmental parameters combined with differences in host use would likely influence dispersal rates.

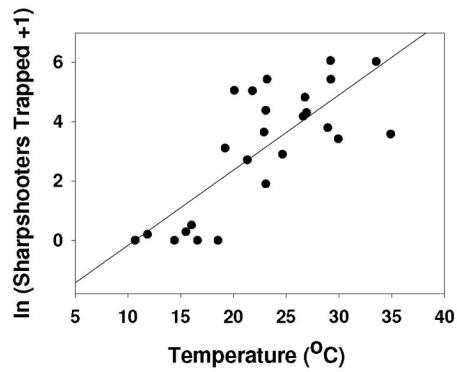

Fig. 4. Mean number of *H. vitripennis* trapped on yellow sticky traps relative to temperature (°C).

In the citrus grove, we found some similarities to the open landscape in terms of movement. Sharpshooters were trapped at the furthest distances and at the highest trap elevations, but few were trapped at the furthest distance until 72 h after release in the citrus setting. The speed at which they reached these distances was more difficult to determine because a much lower percentage (1.7% at 72 h and 2.4% at 744 h) was recaptured; however, for those trapped, it took ≈12 times longer for them to reach the most distance traps in the citrus setting. Linear regressions of the 72-h recapture data with the diffusion model provided significant fits to the data with high coefficients of determination for five of six releases. Both studies indicated that the movement of *H. vitripennis* from a central release site over short and longer periods could be explained by a diffusion process, the speed of which was greatly influenced by the structural complexity of the citrus and/or the insects response to this host in terms of its feeding, mating, and oviposition behaviors. To determine whether the slower movement in citrus was caused by its structural complexity or insect behavior, additional studies in a structurally complex host that is not considered to be a good host for adults (i.e., *Photinia* or *Euonymus;* Daane and Johnson 2002) would need to be conducted. In terms of the environmental parameters that influenced sharpshooter movement in the orchard setting, we found that only temperature had a significant effect. Few sharpshooters were trapped when temperatures fell below 18°C. This is consistent with findings for other closely related sharpshooters whose flight threshold was near 17°C (Purcell and Frazier 1985, Feil et al. 2000).

We also compared the efficiency of IgG and fluorescent dusts in this setting, and while these two techniques were comparable up to 72 h after release, they varied greatly at later recaptures. In our previous study, the IgG proteins were detectable in 90% of the sharpshooters 19 d after marking (Blackmer et al. 2004). In the citrus setting, at 17 d (408 h), the protein was only detectable in ≈35% of the individuals that were positive for fluorescent dusts and therefore should have been positive for the IgG proteins. The reason for this decrease in efficiency cannot be accounted for by differences in weather. Transfer of IgG protein between individuals may have occurred in our previous study where groups of five individuals were held in sleeve cages for the duration of the study. Although a small percentage (4.2%) of the randomly selected sharpshooters trapped on sticky cards were found to be marked with only IgG proteins when they should have been marked with dusts, the dusts were retained better on *H. vitripennis* over the 4-wk recapture period in this setting. This is in stark contrast to the results reported in Hagler (1997b) for marked *Hippodamia convergens* Guérin-Méneville, where chicken and rabbit IgG were retained on the majority

of beetles for 30 d, whereas dust was only retained for ≈1 wk.

Our findings have important implications regarding the movement of *H. vitripennis* across the heterogeneous landscapes they encounter. The landscape between host plants, structural complexity of the host or host matrix and topography could influence temperature and wind gradients and would all be important variables to consider in area-wide management programs. We determined that host plant structural complexity and/or the insects' response to the host plant slowed *H. vitripennis* movement as indicated by the fact that it took nearly 12 times longer for individuals to reach the furthest traps in the citrus setting compared with the abandoned alfalfa setting; however, both studies were conducted under high insect density situations; conditions that for other insects enhanced flight activity (Perez-Mendoza et al. 1999). It is possible that movement might be further reduced under low-density situations. Because citrus can act as both a source and a sink for *H. vitripennis*, this will be an important area of investigation for future studies.

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